Observations on Primary and Secondary Parasitoids of California Oakworm, *Phryganidia californica*, Pupae
(Lepidoptera: Dioptidae)

David J. Horn[1]
Department of Entomology, The Ohio State University, Columbus 43210

Introduction

The California oakworm, *Phryganidia californica* Packard, periodically defoliates evergreen and deciduous oaks (*Quercus*) in coastal California. In the San Francisco Bay region, irruptions occur at 4- to 7-year intervals and last 2–3 years each, followed by spectacular declines in numbers. The oakworm normally has two generations a year. Larvae overwinter on evergreen oaks, particularly coast live oak, *Quercus agrifolia* Née, and feed on new foliage in April and May. Pupation occurs as a chrysalid on branches and trunks of oaks, and in surrounding vegetation, during June. The weak-flying adults emerge in a few weeks, mate, and oviposit on both evergreen and deciduous oaks, especially *Q. lobata* Née, valley oak. Eggs hatch, and larvae feed in July and August, to pupate in September and emerge as adults in October and November. These oviposit on evergreen oaks, eggs hatch, and the larvae may feed but are usually inactive until the onset of warmer weather and new foliage in late March and April (Harville, 1955, and my observations).

Early workers (Kellogg and Jack, 1895; Doane, 1912) attributed oakworm population declines to parasitization because dense infestations usually yielded high percentages of parasitized oakworm pupae. Harville (1955), following exhaustive field study in which pupal parasitism never exceeded 75%, concluded that population declines were caused by a variety of factors, particularly cold winter weather killing overwintering larvae.

Among the pupal parasitoids, Harville found *Itoplectis behrensii* (Cresson) most commonly. It is probably an obligate parasitoid of oakworm pupae (though Muesebeck et al., 1951, cite its presence also in *Recurvaria milleri* Busck). It is bivoltine, like its host, and the long-lived adults can be collected throughout the year (Townes and Townes, 1960). Harville (1955) observed that *I. behrensii* females hunt tactilely on oak branches and trunks, "stumbling" onto potential hosts, and being unable to distinguish previously parasitized hosts. He found that

[1] Formerly Department of Biological Science, California State University, Hayward.

TABLE 1. Population density, parasitization, and survival of *Phryganidia californica* pupae. Hayward, Alameda Co., Calif. May–July.

Year	Pupae/ft^2	Sample size	Total parasitization	Moth emergence
1969[1]	23.4	270	110 (41%)	100 (37%)
1970	30.3	478	339 (71%)	56 (12%)
1971	.01	15	2 (13%)	12 (80%)
1972	0.4	35	2 (6%)	26 (74%)

[1] Sampling commenced 20 June. Parasitization probably lower, and moth emergence greater, for whole season, than indicated value.

I. behrensii in turn was parasitized by 3 secondary parasitoids: *Gelis tenellus* (Say), *Mastrus aciculatus* (Provancher), and *Dibrachys cavus* (Walker); the total incidence of parasitism by all three on *I. behrensii* was less than 1% in eight study sites though *D. cavus* was sometimes locally more abundant. Harville also found *Brachymeria ovata* (Say) as a primary pupal parasitoid of the oakworm. It has no secondary parasitoids. *B. ovata* is facultative, having been recorded from over 100 species of lepidopterous pupae (Burks, 1960), and Harville suggested that it might survive on alternate hosts, possible species of *Malacosoma*, during times of oakworm scarcity.

My preliminary observations of oakworm and parasitoid populations near Hayward, California in 1969 revealed more extensive secondary parasitization of *I. behrensii* than that Harville reported. This suggested that the interrelationships between oakworm populations and those of the several parasitoid species warranted further study.

METHODS

I selected a wooded hillside adjacent to the Ecological Field Station, California State University, Hayward. The vegetation of the study area, described in detail by Cogswell (1966) is a broadleaf evergreen woodland, dominated by coast live oak and California laurel (*Umbellularia californica*). No insecticides have ever been used here. In 1969–70, but not in 1971–72, the spring generation of oakworms severely defoliated oaks in the study area.

On each visit to the study plot in 1969–70 and 1972, I counted fresh oakworm pupae in each of 10 1ft^2 areas of tree-trunk undersurface chosen randomly from a group of 5 trees. Pupae were so few in 1971 that I obtained no meaningful estimate of density.

I determined the extent of parasitism by collecting a sample of 50–

Table 2. Emergence of parasitoid species from *Phryganidia californica* pupae. Hayward, Alameda Co., Calif. June–July 1969, May–July 1970.

Year	Total parasitoids	*I. behrensii*	*B. ovata*	*G. tenellus*	*M. aciculatus*	*Bathythrix*	*D. cavus*[1]
1969	110	32	9	21	1	5	42[1]
1970	339	107	19	66	6	69	72[1]

[1] Number of hosts parasitized, not number of emerging parasitoids. *D. cavus* is gregarious, with 3–10 parasitoids/host.

100 pupae randomly from lower, accessible, oak limbs and trunks, and kept pupae individually in 4-oz jars until moths or parasitoids had emerged. I repeated the procedure every 5 days from the onset of pupation until no new pupae appeared. Pupae from which nothing emerged were visually inspected, then dissected. While collecting pupae, I spent several hours observing the activities of *I. behrensii* and *B. ovata*. When I encountered pupae of other Lepidoptera, I saved these for possible parasitoid emergence. These were primarily *Hemerocampa vetusta* Boisduval (Liparidae), *Hemihylaea edwardsi* Packard (Arctiidae), *Malacosoma californicum* (Packard), and *M. constrictum* (Edwards) (Lasiocampidae).

Results

Six species of parasitoids emerged from field-collected oakworm pupae; 5 were those Harville (1955) found; the sixth, *Bathythrix* sp., a secondary parasitoid of *I. behrensii*, represents a new host record.

Table 1 shows trends in oakworm numbers, pupal parasitization, and moth emergence during 1969–72. Oakworm density and parasitization increased from 1969 to 1970, then the oakworm population declined dramatically. Fewer moths were produced in 1971–72 than in 1969–70, but the percentage produced was much greater.

Table 2 shows relative proportions of the several parasitoid species in 1969–70. Parasitoids of *I. behrensii* were much more abundant in 1970 than in 1969. In 1971–72 I found only two parasitized oakworm pupae each year; all yielded *I. behrensii*. No secondary parasitoids or *B. ovata* were found in oakworm pupae in 1971 or 1972. I reared *B. ovata* from one pupa of *Hemerocampa vetusta* and one of *Hemihylaea edwardsii*. The latter is a new host record. From 35 pupae of *Malacosoma* spp. in 1972, I reared two *G. tenellus* but no *B. ovata*.

Fig. 1 illustrates seasonal trends in the incidence of parasitization

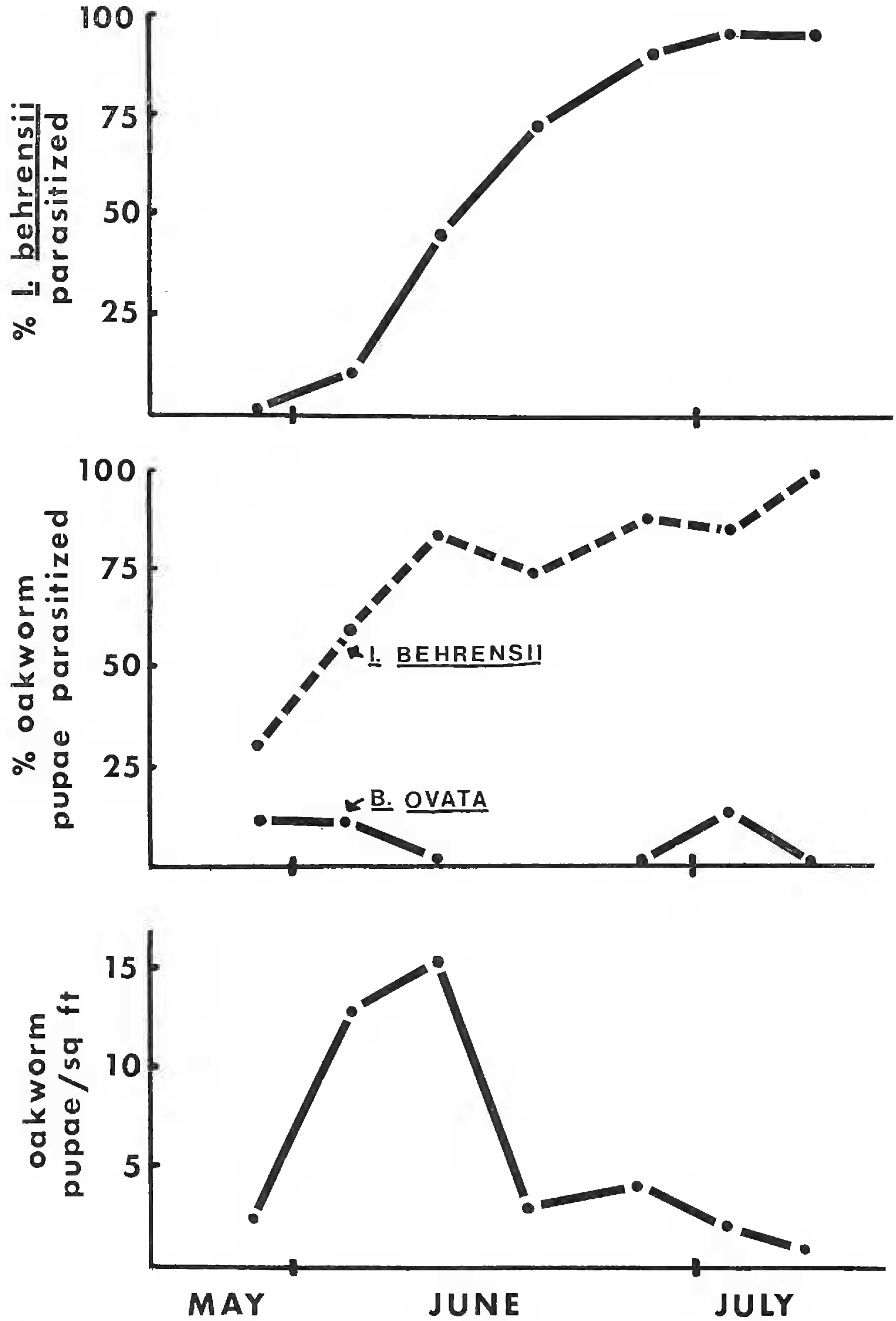

FIG. 1. Trends in oakworm pupal density and parasitization at Hayward, Alameda County, California, 1970.

in 1970, the year for which I obtained most data. Parasitization by *B. ovata*, though never exceeding 10%, was greatest on earlier oakworm pupae, with a small second generation in early July. Percent parasitization by *I. behrensii* increased from 23% in May to over 90% in July. Over the entire sampling period from May to July, oakworm pupal mortality was 88%, as follows: *B. ovata* 4%, *I. behrensii* 67%, and unknown 17%. Some of the unknown mortality may have been due to fungal infections and some may have resulted from oviposition by parasitoids or feeding by predaceous Hemiptera (Horn, 1973). Occasionally, I encountered desiccated parasitoid larvae within oakworm pupae. These are included as unknown mortality because I could not determine the species of parasitoid involved.

The incidence of secondary parasitization of *I. behrensii* increased from 0 in May to 100% in late June and July. *G. tenellus*, *D. cavus*, and *Bathythrix* sp. were equally abundant and showed no seasonal separation, while *Mastrus* was much less common (Table 2). Together, secondary parasitoids killed 69% of *Itoplectis* present in the samples over the season. A few *B. ovata* may have been parasitized in early July.

I observed searching behavior of 10 *I. behrensii* females in 1970 for periods up to 45 minutes each. My observations agreed with those of Harville (1955), that *I. behrensii* searches very rapidly and efficiently, running over the branches and trunk, and ovipositing readily in previously parasitized hosts. In every case, females turned away when encountering their own trail, indicating the presence of a trail odor (Price, 1970). Two *B. ovata* females that I observed moved about more slowly than *I. behrensii* and oviposited in nearly all oakworm pupae encountered. One moved directly from an oakworm pupa to oviposit in a cocoon of *H. vetusta.* Superparasitism apparently occurs readily in each species.

Discussion

Conclusions based upon observation of a local population through only a portion of a cycle are tentative at best, but the increase in parasitization immediately preceding the oakworm population decline suggests that *I. behrensii* may be partially responsible for oakworm population declines.

Of interest are the interactions among the parasitoids and their use of a fluctuating resource. *I. behrensii,* having no alternate hosts, must disperse readily and search quickly, as its probability of survival is low, especially in years when oakworm pupae are scarce. It averages twice the size of *B. ovata*, has much longer wings, and adults are relatively long-lived. Other parasitoid species display these characteristics in unstable environments (Price, 1972). *B. ovata*, being facultative, moves to alternate hosts, at least to *Hemerocampa vetusta* and *Hemihylaea edwardsii*, when oakworms are scarce. It is smaller and stockier than *I. behrensii* and is thus capable of searching a wider variety of habitats, including ground litter and bark crevices, as well as the surfaces of branches and trunks. This befits a parasitoid with over 100 recorded hosts. *Malacosoma* may not be as likely a reservoir of alternate hosts as Harville (1955) suggested. I did not find *B. ovata* in a small sample (N = 35) of *Malacosoma* pupae, nor did Langston (1957) discover it in a large survey of parasitoids of California *Malacosoma*, though Stehr and Cook (1968) recovered it from *Malacosoma* elsewhere.

I. behrensii thus has some attributes of an r-strategist whereas *B. ovata*, relatively, is a K-strategist (Force, 1972); populations of the former fluctuate in number along with their fluctuating resource, while numbers of the latter probably remain relatively constant due to the supply of alternate hosts. *B. ovata* occurs earlier and later than the bulk of *I. behrensii* in oakworm pupae. This suggests that *I. behrensii* may be the superior competitor when both species parasitize a single host pupa. In the laboratory I attempted to induce females of each species to oviposit in each of 20 oakworm pupae, from which I recovered 14 *I. behrensii* and 5 moths. However, I was not certain whether that *B. ovata* actually oviposited, so the results are inconclusive.

The facultative secondary parasitoids, at least *Gelis tenellus* and *Dibrachys cavus*, also move to alternate hosts including parasitoids of *Malacosoma* (Langston 1957) when *I. behrensii* is rare. *Mastrus aciculatus* has been recorded from several hosts, mostly Tenthredinidae (Bobb 1965, Price, 1970), as have species of *Bathythrix* (Muesebeck *et al.* 1951). There was no seasonal separation of their occurrence on *I. behrensii*, but they do differ in size and this may affect competition among them. More must be known of their relative abundance on other hosts to ascertain their competitive interactions, which may be rapidly changing. For instance, *Bathythrix* occurred commonly in my 1970 field samples yet was not present in any of Harville's study populations. It may have recently broadened its host preference to include *I. behrensii*. The total incidence of parasitization on *I. behrensii* by all 4 secondary parasitoids (52% in 1969 and 69% in 1970) was far greater than the 1% reported by Harville (1955). This suggests that significant local changes may occur in the parasitoid complex of the oakworm, with potentially important consequences for its population dynamics.

ACKNOWLEDGMENTS

The work was partially supported by a grant from the Research Foundation, California State University, Hayward. C. E. Dasch assisted with identification of parasitoids. R. S. Horn helped search for host pupae and she and J. P. Harville read drafts of the manuscript. The insatiable appetites of C. A. and R. B. Horn kept me abundantly supplied with 4-oz jars.

LITERATURE CITED

BOBB, M. L. 1965. Insect parasite and predator studies in a declining sawfly population. J. Econ Entomol., 58: 925–926.

BURKS, B. D. 1960. A revision of the genus *Brachymeria* Westwood in America North of Mexico (Hymenoptera: Chalcidae). Trans. Amer. Entomol. Soc., 86: 225–273.

COGSWELL, H. L. 1966. Thirtieth breeding bird census 40. Broadleaf evergreen forest with shrub-filled openings. Audubon Field Notes, 20: 637–643.

DOANE, R. W. 1912. Some insect pests of the California live oaks. J. Econ. Entomol., 5: 346.

FORCE, D. C. 1972. r- and K-strategists in endemic host-parasitoid communities. Bull. Entomol. Soc. Amer., 18: 135–137.

HARVILLE, J. P. 1955. Ecology and population dynamics of the California oak moth *Phryganidia californica* Packard (Lepidoptera) Microentomol., 20: 83–166.

HORN, D. J. 1973. *Leptocoris rubrolineatus*, an occasional predator of the California oakworm, *Phryganidia californica*. Pan-Pac. Entomol., 49: 196.

KELLOGG, V. K. AND F. J. JACK. 1895. The California phryganidian. Proc. Calif. Acad. Sci. (Ser. 2), 5: 562–570.

LANGSTON, R. L. 1957. A synopsis of hymenopterous parasites of *Malacosoma* in California. Univ. Calif. Publ. Entomol., 14: 1–50.

MUESEBECK, C. F. W., K. V. KROMBEIN AND H. K. TOWNES. 1951. Hymenoptera of America north of Mexico. Synoptic catalog. USDA Agr. Monog., 2: 1–1420.

PRICE, P. W. 1970. Trail odors: recognition by insects parasitic on cocoons. Science, 170: 546–547.

PRICE, P. W. 1971. Parasitoids utilizing the same host: adaptive nature of differences in size and form. Ecology, 53: 190–195.

STEHR, F. W. AND E. F. COOK. 1968. A revision of the genus *Malacosoma* Hubner in North America (Lepidoptera: Lasiocampidae): systematics, biology, immatures, and parasites. U.S. Nat. Mus. Bull., 276: 1–321.

TOWNES, H. AND M. TOWNES. 1960. Ichneumon flies of America north of Mexico. 2. Subfamilies Ephialtinae, Xoridinae, Acaenitinae. U.S. Nat. Mus. Bull., 216: 1–676.